THE TENDENCY TOWARD PROGRESSION OR PERFECTIVE DEVELOPMENT IN PLANT EVOLUTION

STUDIES IN DETERMINATE EVOLUTION NO. IX

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After any extensive study of certain fundamental characters or processes in a general taxonomic plant series, a very remarkable tendency becomes evident in that when a new reaction is introduced into the evolutionary movement, it is often much less definite and certain at first than it becomes in forms which plainly belong to a higher general level of organization. This movement toward perfection was evidently recognized long ago by Aristole who must be regarded as a genuine evolutionist. He said that: "Nature produces those things which, being continually moved by a certain principle contained in themselves, arrive at a certain end."

Among the first or perhaps the first of the modern evolutionists to declare an internal force or cause for evolution was the botanist Naegeli. He postulated an internal or innate tendency toward progression and perfect development or a so-called principle of perfection in the evolutionary process, and because of this tendency, according to Naegeli, organisms are constantly varying in such a manner as to rise in the scale of nature.

According to Naegeli, the fact of a progression in the past requires an internal tendency to rise. Darwin's answer to this was that natural selection would also imply progression. But it is evident that if the progression from a lower to a higher, from a less perfect to a more perfect condition were caused by selection, the whole series should not be present but only the more perfected; for the selection of the fittest implies the elimination of the unfit. There can be no selection without elimination. Thus the fact of endless numbers of close, progressive series is a direct refutation of both Lamarkism and Darwinism, since the entire series may be present in the same general environment. A careful study of the taxonomic

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system also shows that many of the most definite group characters can have no special adaptative value, can have no special use whatsoever. Whether a flower has a trilocular, bilocular, or unilocular ovulary can be of no special advantage either to the biological relations of the individual or to the individual in relation to its physical environment. Very generally the progressive phylogenetic series does not at all correspond to any ecological zonation. If Lamarkian evolution were in operation, the series should correspond with ecological zonation of habitats, regions, altitudes, latitudes, and other ecological conditions. There plainly is no such correspondence. Furthermore, our recent knowledge of mutation shows that evolution proceeds through individuals and not through the race in general, otherwise the old race would have to disappear in the evolution of the new, and there could not be a series of closely related groups.

Of course, it is evident that if there are orthogenetic series and that they have no general relation to corresponding environmental conditions, the very fact of such orthogenetic series shows that a progressive or perfective principle is involved, and this would not be dependent on the order of appearance or relationships of the units evolved in the series. The fact of the series is immediately of more importance than the order of its production. The progressive movements may be useful or not, or they may even occasionally be decidedly disadvantageous to the individual but may nevertheless continue because associated with compensating conditions. On every hand, one meets structures that the idealist would immediately pronounce perfect as compared with less elaborated types farther down the series. What we wish to consider is the fact that very many evolutionary progressions do become more perfect as one advances in the ascending scale of organism and structure. There is not only improvement, step by step, but the reaction becomes more decided, more definite, more prompt, until failure of expression is practically impossible unless something entirely new is added to the system, which may interfere with the given reaction. This evolutionary improvement of a given reaction must be due to one of two causes, either the structural elements of the protoplasm on which the reaction depends become more perfected in their mechanism or else a greater number of similar units, having the same influence in growth and hereditary expression, are

produced whose combined influence then gives a more vigorous and more dependable action.

In recognizing the fact of a progressive, perfective process and principle in the evolution of potentialities, one is not to postulate or subscribe to an "entelechy" or "elan vital" as an hypothesis to cover our present profound ignorance of the real nature and structure of the protoplast and its evolution. It is sufficient, at present, to study the actual series and their direct implications, which if properly done will keep biologists busy for some time without indulging in speculations for which we have had, up to the present, no adequate accumulation of proper investigations. We know that the evolution of the automobile, for example, is due to the creative activity of the human mind, but we do not on that account endow the automobile with a mind or evolutionary force, to explain the intricacies of its organization. The quest for ultimate causes or an Ultimate Cause does not belong directly to the realm of science but is a philosophical-theological discipline. From the very nature of the case no scientific causal explanation of evolution is possible.

The old unscientific, causal, evolutionary hypotheses, like "chance" or "fortuitous variation," "direct action of the environment," "use and disuse," and "natural selection" must be disregarded and allowed to die a natural death, because they are not only unscientific but are contradicted on every side by the realities of the taxonomic systems; as becomes evident when these are studied in their entirety and in relation to their ecological conditions. Some would-be philosophical scientists are still under the delusion that evolution is primarily concerned with the "origin of species." Speciation has little to do with the real problem of evolution as O. F. Cook pointed out over thirty years ago.

PROGRESSION IN DEFINITENESS OF DIFFERENTIAL EXPRESSION IN SPOROPHYLL AND FOLIAGE LEAF

In the lower ferns there is no apparent difference between sporophyll and sterile foliage leaf except that the former produces sporangia on its surface and the latter does not. But as one follows out certain evolutionary lines, a very decided dimorphism gradually appears until the two leaves may have very different aspects and characteristics. Thus in *Onoclea sensibilis* L., belonging to the Polypodiaceae, we have rather

an extreme example of dimorphism. This fern shows its advanced character also in having unisexual gametophytes instead of the usual hermaphroditic condition. Now, although the dimorphism is decided, intermediate expressions between sporophylls and foliage leaves are frequently found, and these appear in all gradations from one extreme to the other.

In the Osmundaceae, which represent the lowest family of the Filicales, a rather similar evolutionary movement has taken place. In *Todea barbara* Moore there is little difference between the pinnae which bear sporangia and those which are sterile. But in the extreme species, *Osmunda cinnamomea* L., the dimorphism between foliage leaf and sporophyll is nearly as decided as in Onoclea. Here again intermediate expressions are quite common and it is not difficult to find leaves that are halfway expressions between the two. Apparently a very little disturbance in the ecological-physiological conditions in which the protoplasts are functioning causes a confusion in the hereditary reaction system. Now, as one goes up the phylogenetic scale into the higher plant series one finds not only that there is a still greater dimorphism between foliage leaf and sporophyll but also that intermediate expressions are exceedingly rare or practically nonexistent. It is only when unusual mutative changes have occurred that intermediate expressions may again appear and these, of course, are then not the result of fluctuating expressions. In the highest plants the physiological processes which give rise to the one expression or the other begin in a definite direction and continue thus to the end of the development of the given leaf, whether sporophyll or foliage leaf.

EVOLUTION OF DEFINITENESS OF DETERMINATION OF THE FLORAL AXIS

The lowest flowers, which represent the first stages of determinateness of the reproductive sporophyll-bearing axis, illustrate the principle of perfective evolution in a very convincing manner. In the lowest living vascular plants, as in the lower lycopods and ferns, the reproductive axis is entirely indeterminate, giving rise indefinitely to successive zones of foliage leaves and sporophylls. From this primitive condition the flower, or determinate sporophyll-bearing shoot, has evolved. The causal factor, therefore, for flower production is determinateness of the reproductive bud. Some potentiality is added

to the protoplast which induces the determinate growth and final death of the bud involved. Now the remarkable thing about this floral evolution is the fact that at first, in the lower levels, the factor or factors of determination act very slowly so that large numbers and usually very variable numbers, are produced before determination of the flower is accomplished. Again, just as in the foliage leaf, the determinate action is frequently inhibited. A small deviation from the normal physiological gradient is enough to induce failure of the determination potentiality and proliferation is the result. In other words, the reproductive bud fails in its determinate process and indeterminate growth continues beyond the reproductive zone just as in plants which have not acquired the reproductive determinate potentiality. The potentiality cannot be depended upon. Proliferation is quite frequent in such low homosporous flowers as *Lycopodium obscurum* L. and *L. complanatum* L. It is also very abundant in some of the lower species of the Equiseta, namely, in *Equisetum fluviatile* L. Frequently also a second cone appears at the end of the proliferated axis, and this second cone may proliferate again. Proliferation of the flowers is frequently seen in some of the lower living conifers, as in both staminate and carpellate cones of *Araucaria angustifolia* (Bert.) Ktz. and the carpellate cones of *Cunninghamia lanceolata* (Lamb.) Hook. The carpellate cones of *Larix kaempferi* (Lamb.) Sarg., *L. decidua* Mill., and *L. laricina* (DuR.) Koch. proliferate occasionally. Proliferation of the flower is also met with occasionally in low types of angiosperms, as in species of Ranunculus, Rosa, and Pyrus. Now in passing along any of the main evolutionary flower series one finds that the determination becomes continually more prompt until at the ends of the series only a few floral parts are produced, in the extreme cases only one, before determination is completed and also that the number of parts is practically without fluctuation. Furthermore, the possibility of proliferation as an ordinary fluctuation is practically eliminated. The determinate reaction gains on the ontogenetic progression, step by step, through the general evolutionary series, in all lines, until in the extreme types the limit is reached when the center of the reproductive bud stops in its growth even before a single incept of any lateral floral organ is in evidence. The evolution of completeness, promptness, and reliability of determination is most remarkable when compared with the variability and

unreliableness of determination in the primitive types of flowers. The failure of prompt determination in the lower types of flowers is also shown in a special way in such groups as Equisetum and Zamia. In the lower species of Equisetum there is a prominent vegetative point at the tip of the cone. In the more advanced series, this point disappears through the more prompt action of the determinate process after the reproductive reactions cease. In *Zamia furfuracea* L. f. also there is a prominent vegetative point on the carpellate cone, associated with a very variable spiral system, while in the higher conifer levels as in *Sequoia washingtoniana* (Winsl.) Sudw. the carpellate cone, which has a 3–5–spiral system but a much more shortened floral axis, has no such point developed. We see then that the evolution of the flower is a vivid demonstration of the perfective principle in evolution, since the reaction advances from a slow movement to a very prompt movement, from a variable action to a mathematically exact reaction, from a frequent failure of action to a dependable action with failure reduced to zero.

IMPERFECT DETERMINATENESS IN CERTAIN INFLORESCENCE HEADS

In the evolution of the inflorescence to a head, there may be the same lack of prompt determination of the inflorescence axis in the lower species as has been seen in the case of the flower axis. If one studies the evolutionary series in which racemes or panicles are the prevailing types but which have at the end just attained to the condition of having head inflorescences, proliferation is a frequent phenomenon. Thus in the Lamiaceae, the more common condition is to have the flowers axillary, or in racemes, panicles or spikes. In a few genera, however, heads have evolved, as in species of Koellia and Monarda. *Koellia pilosa* (Nutt.) Britt has proliferated heads occasionally and both *Monarda fistulosa* L. and *M. didyma* L. have been seen to proliferate frequently. The Dipsacaceae represent one of the lower families of the Compositales in which great group the inflorescence shows evolution from an elongated head to a very flat disk. Such inflorescences as those of Dipsacus and Scabiosa represent the lower levels while Aster and Leontodon are on the advanced level of disk development. *Scabiosa atropurpurea* L. has frequent proliferation of the head while such a condition is not developed in

the higher Helianthaceae and Cichoriaceae. Again as in the flower, the proliferation of the more primitive heads indicates that the beginning of any important evolutionary movement is usually less stable and less dependable than the more advanced developments in the same phyletic line.

PEDUNCLES AND PERIANTHS IN EQUISETUM

In the lower vascular plants with primitive flowers, there are no special hereditary potentialities that can come into play in the transition zone between the vegetative axis below and the reproductive axis above, but as we ascend the evolutionary ladder the protoplast acquires a greater and greater accumulation of hereditary potentialities, some of which will be of such a nature as to be thrown into activity on this transition zone. Thus peduncles and perianths soon come into prominence although the lowest species have no such structures. In Equisetum a sterile calyx is thus evolved. In the lowest species of Equisetum the calyx whorl has sporangia in its segments on the upper side while in the higher types, like *E. scirpoides* Mx. and *E. arvense* L., it is completely sterile. But since the evolutionary movement in this respect is not very far advanced, about one out of about every 20 cones in *E. arvense* will have one or more sporangia on the calyx. In a high type of flower, like a Geranium or a lily one would have to hunt a long while before a flower appeared with sporangia on the perianth segments. Only with a special evolution, like a very rapid advance of the time of flower determination in the ontogenetic sequence, would it again be possible to have a confusion of this kind. In Equisetum also the reactions which produce sterile and fertile shoots are not very strongly determined and thus every degree of semisterile cone between a perfect cone and vegetative tip may be easily found in most species. Again in the highest species of Equisetum, *E. arvense*, these intermediate cones are quite rare. The bud usually produces a fertile shoot with a normal cone or a sterile shoot with a vegetative tip. In the higher flowering plants such intermediate developments do not occur unless as the result of extreme mutations or some such special cause. The factors which are responsible for floral shoots or leafy shoots act promptly and decidedly so that no half-way structures are produced unless a decidedly disturbing, new hereditary potentiality has previously been introduced into the system. The lowest species of Equisetum

have no definite peduncle developed below the cone while in the higher a very variable peduncle is present. In *E. arvense* the peduncle may fluctuate from one-fourth inch to more than five inches in length.

PROGRESSION FROM FIVE-PARTED TO FOUR-PARTED FLOWERS IN DICOTYLS

Although a few of the dicotyl series begin with a trimerous system in the flower, the general rule is a pentamerous type as the basal structure. Frequently then there is a direct mutation to the tetramerous type. In this common progressive change the principle of perfective evolution is also prominently in evidence. A few selected examples are given below. In the Celastraceae, *Celastrus scandens* L. has the usual five sepals, five petals, and five stamens. In the genus Euonymus, the flower has mutated to the four-part condition. Now in *E. obovatus* Nutt., the sepals, petals, and stamens are usually five each; but occasionally a four-parted flower is produced beside the five-parted ones. A mutation has been accomplished in the species but this new factor acts only occasionally in a special physiological condition which arises in the same cell complex as the condition which leads to five-parted flowers. In *E. atropurpureus* Jacq., the flower is usually four-parted, but sometimes five-parted flowers are produced along with the four-parted in the same cluster. In *E. europaeus* L. and *E. alata* Regel, the flowers are four-parted and only rarely is a five-parted flower developed on the plant. Finally in a related genus, in *Pachystima canbyi* Gr., the flower is regularly four-parted with four sepals, four petals, and four stamens. The potentialities responsible for the four-parted reaction have become perfected so that there is no failure.

Ruta graveolens L. has four-parted flowers, but usually the central flower of each main branch of the flower cluster has a five-parted flower. The mutation does not work in the central gradient. The Tubiflorae are characteristically a group with pentamerous flowers and this is true for part of the Gentianales, but in the Oleaceae, the flower has mutated to a four-parted perianth. Now in the common lilac, *Syringa vulgaris* L., although the flowers are mostly of this type, very many of the panicles show flowers with a five-parted perianth, usually at the end of the panicle or toward the center of some of its branches. In mutating to the four-parted condition, the plant

did not loose the potentialities which produce five-partedness. Occasionally a three-parted flower is produced. The factors which change the reaction of the flower bud from a five-parted to a four-parted condition bring about a further reduction, which indicates that a further mutation might occur which would give rise to a three-parted lilac. In the golden-bell (Forsythia), five-parted flowers are less common than in the lilac.

The Crassulaceae also show a fundamentally pentamerous condition of the flower, but with a strong tendency to mutate to a tetramerous condition. Many of the genera have flowers of both types. Some of the genera have five-parted flowers regularly. In *Sedum triphyllum* (Haw.) S. F. Gray and *S. telephioides* Mx., the flower is five-parted, while in *S. acre* L. and especially in *S. ternatum* Mx. the central flower of the cyme is commonly five-parted while those on its branches are four-parted. Thus again, in Sedum we see a mutation to a four-parted condition but the factors involved are not in such a state as to completely prevent the more fundamental pentamerous potentiality from being expressed in certain parts of the inflorescence.

THE PERFECTIVE TENDENCY IN THE EVOLUTION OF ZYGOMORPHY

The lower types of flowers, whether spiral or cyclic, are all radially symmetrical. On the higher levels in most lines of monocotyls and dicotyls, zygomorphy appears and sometimes becomes very extreme. The most fundamental movement in the evolution of zygomorphy is the more prompt determination of one side of the determinate flower bud than the other. Along with this progressive movement, usually, various factors of shape, color, texture, ornamentation, etc., are evolved. As stated, zygomorphy is usually not encountered until the series has advanced to a considerable degree of complexity. However, occasionally a distinct zygomorphy is found even in the primitive spiral stage. Thus in *Pinus radiata* D. Don., *P. muricata* D. Don., *P. attenuata* Lem., *P. sabiniana* Dougl. and other species a decided zygomorphy is produced by the difference in character of the ovuliferous scales on the inner and outer sides. Although the pine cone is a low type of flower it, nevertheless, does have a high degree of complexity of reactions when compared with such simple systems as are

presented by the cones of Lycopodium, Zamia, or Araucaria. In the dicotyls, a prominent development of zygomorphy is known in some genera of Ranunculaceae which represent a very low condition otherwise. The flowers of Aconitum and Delphinium have not advanced beyond the apocarpous stage, yet zygomorphy is pronounced in both calyx and corolla.

The evolution of zygomorphy, like other fundamental movements, shows a decidedly progressive and perfective sequence in many series. Thus a series of genera or species may show a progressive reduction of stamens from 6 to 5 to 3, and then to 2 or to 1; or from 5 to 4 to 2, to 2 halves. In the Scitaminales, Ravenala has 6 stamens, which is the fundamental number for all the Liliiflorae whether hypogynous or epigynous. It has a slight zygomorphy but not enough to eliminate any of the stamens. In its near relative, the banana, *Musa sapientum* L., one stamen is missing in both staminate and carpellate flowers. There is simply an empty space where the stamen should appear on the zygomorphic plane. Now on almost any bunch of banana flowers one can occasionally find this sixth stamen developed in one or more flowers. It may be a perfect stamen or a vestige of any degree of expression. The banana flower has only taken the first step of sufficient size to eliminate one stamen and the condition is not perfected in relation to the general reaction system, and so frequently the original condition is produced which gives six stamens. A little disturbance in physiological condition brings back the original structural type. In the higher Scitaminales there are but five stamens or sometimes only three, all except one of which are changed to showy staminodes. In the two highest families, Cannaceae and Marantaceae, there is an unsymmetrical potentiality introduced which also affects the remaining fertile stamen which is then reduced to a half fertile stamen. The whole flower is now bilaterally unsymmetrical but still shows its complete evolutionary history in its make-up—(1) spiral symmetry, (2) cyclic symmetry, (3) zygomorphic symmetry, (4) inequilateral condition. So far as the andrecium is concerned the evolutionary sequence has attained to its definite determinate limit at the one-half stamen condition. In the Orchidales zygomorphy also brings about a reduction of the stamens from six to one, the very vast majority of orchids, 10,000 or more, having this one stamen in the same position on the zygomorphic plane in relation to the other

parts. Those who still think that there is any fortuity in the fundamental processes of evolution should study the structural relations of this one stamen in the Orchidaceae.

In the Scrophulariaceae there are various zygomorphic reduction series, the stamens running from five to four to two. In the Bignoniaceae, Bignonia, Anisostichus, and Tecoma have four anther-bearing, didynamous stamens with a vestige of the fifth. Paulownia shows the same condition. But in Catalpa the anther-bearing stamens are reduced to two, through the advancement of the zygomorphic evolution, with three prominent vestiges. Now just as in the banana, the two lateral, reduced stamens, especially in *Catalpa speciosa* Ward., sometimes develop normally, giving flowers with four stamens. Occasionally all five stamens develop normally. These four- or five-stamened flowers appear in the panicles along with the characteristic two-stamened flowers. It is not a matter of segregation of old heredity from new heredity but rather the expression of an old suppressed heredity over a more recently acquired heredity potentiality through some local change in physiological activity.

In the Lamiales, the lower types again show the fundamental number of five functional stamens. Then in the Lamiaceae, Isanthus has four didynamous stamens and this is the usual condition of most of the intermediate genera, while Monarda and Blephilia have but two. Finally in Salvia the zygomorphic advancement is extreme and not only gives a zygomorphic calyx and an extremely zygomorphic corolla, but the two remaining stamens also are decidedly affected by the zygomorphy and show a progressive advance so that in the higher species each stamen has but a half anther, the other half being transformed into a peculiar lever-handle. The zygomorphic evolution has advanced to the last possible degree of perfection in so far as it can affect the stamens.

The general trend toward a perfective advancement in the evolutionary process is also prominently shown in the zygomorphic conditions of the closely related families, Cistaceae and Violaceae. The Hypericaceae represent a more primitive, actinomorphic group belonging to the same general series. In Crocanthemum, the flowers have an actinomorphic aspect, but close examination shows that the two outer lateral sepals are smaller and narrower, or sometimes wanting. In Cubelium the flowers are only moderately zygomorphic, the petals being

nearly equal. The lower one is, however, somewhat gibbous, but the andrecium and calyx show little or no zygomorphy. In Viola the zygomorphy becomes successively more and more extreme until in such species as our common blue violet, *Viola papilionacea* Pursh, the petaliferous flowers are extremely zygomorphic, having three distinct types of petals, two very distinct types of stamens and even a somewhat zygomorphic calyx and gynecium. Those who have thought that such a series was produced by natural selection because of the highly specialized character of the flower, with its nectar spur, adapted for insect pollination, should certainly be shocked to find that these highly perfected, zygomorphic, insect-attractive flowers are either completely sterile or produce very few seeds, while the later-developed, cleistogamous flowers, which have no corolla whatever and are entirely self-pollinated, are abundantly fertile and produce great quantities of perfect seed. Such cleistogamy is found in many genera of both anemophilous and entomophilous plants. It is plain that the perfection of the zygomorphy and the showyness of the petaliferous flower were evolved neither through any selective action of visiting insects or other environmental conditions nor through any direct response to an unusual physical environment. One might remark in passing, that to the crude pseudo-science of the past century, such a zygomorphic, showy corolla as is present in the higher types of violets was conclusively an "attractive adaptation to fertilization" and the irregularity of the zygomorphic shape was to provide a suitable landing place for the visiting insects. The evolution of zygomorphy in the Violaceae is accompanied by another interesting development, namely, the elongation of the flower peduncle. In *Cubelium concolor* (Forst.) Raf. the peduncle is ¼–¾ inches long; in *Viola canadensis* L. 1–2 in.; in *V. eriocarpa* Schw. 1½–3 in.; in *V. conspersa* Reich. 2–4 in. These species have aerial leafy shoots while the remaining ones mentioned below have geophilous stems. *V. blanda* has peduncles 2½–5 in. long; *V. cucullata* Ait. 4–7 in.; *V. papilionacea* Prush 4–8 in.

Since there is no advantage to the plant in thrusting its showy flowers up, to the convenience of the pilfering insects, the "adaptation" must be for some other important "use." And in the spring see how readily the children can and do gather these pretty flowers and how "perfectly adapted" they are for making great bouquets! "Adaptation" is a

wonderful thing! In this connection, the "adaptation" to insect pollination of the common milkweeds may be considered. In the Apocynaceae the pollen is glandular, although the pollen-grains are simple, but in the next higher family, Asclepiadaceae, more definite pollinia or granular masses are developed which in Asclepias and other genera become marvelous structures that can only be removed and carried about through the aid of insects. Two flattened, pear-shaped, waxy pollen-masses from two adjacent anthers form a pair suspended on curved threads from a peculiar connective which has a slit in which the proboscis or foot of the unlucky insect is caught and from which it cannot escape without either leaving its leg behind or carrying the whole apparatus with the two pollen-masses away. A more perfect or ingeneous devise could hardly be conceived. Yet this perfected mechanism is so inefficient in inducing pollination of the milkweed flower, that, after a careful statistical study of our common *Asclepias syriaca* L., over a wide extent of territory, it was found that less than one flower in 100, under all ordinary environmental conditions, ever becomes pollinated. The milkweed "adaptation" is about as inefficient a method of pollination as could be devised.

VARIOUS OTHER EXAMPLES OF THE OPERATION OF THE PROGRESSIVE, PERFECTIVE PRINCIPLE

The genus Thalictrum belongs to a family whose flowers are mostly bisporangiate. In Thalictrum, however, there is a gradation series of species running from the perfect condition to a rather decidedly diecious state. *Thalictrum clavatum* D C. has bisporangiate flowers, *T. polygamum* Muhl. usually bears both bisporangiate and monosporangiate flowers. *T. dasycarpum* Fisch. & Lall. is diecious but frequently develops individuals with both kinds of monosporangiate and also bisporangiate flowers, and the sex is easily partially or completely reversed from time to time through ecological control. *T. dioicum* L. is decidedly diecious and individuals with some perfect or completely reversed flowers are comparatively rare. It is also more extreme in its general morphological characters than the other species mentioned. Under experimental control it is also more constant in sex than the other species mentioned above. All species of Thalictrum fall into this series in respect to their sexual conditions. A somewhat similar series is presented by the genus Fraxinus. The genus Acer shows a condition

somewhat similar to Thalictrum. The ancestral type of Acer had bisporangiate flowers as is plainly indicated by the prominent vestigial sporophylls of the opposite sex condition in the flowers of the more primitive species. *Acer plantanoides* L. has prominent petals, nectar glands, large vestiges of the opposite sporophylls, and frequently reverses the sex in either direction, sometimes involving rather large branches. *A. rubrum* L. and *A. saccharinum* L. have small vestiges of the opposite sporophylls but still show frequent sex-reversals, although the phenomenon does not appear to be so common as in *A. plantanoides*. Finally *A. negundo* L., an extreme species in many characters, shows no vestiges of the opposite sporophylls in the flower and also shows sex-reversal very rarely, although such reversal has been reported. There is thus a progressive degree of perfection and constancy in the evolution of the secondary sexual states. Similar conditions have been found in quite a number of other diverse genera, both by observation and by direct experiment. In the genus Acer, there is evident another interesting condition. Acer belongs to a series of groups that are prevailingly tricarpellate. But Acer itself has advanced in the same direction as nearly all advanced dicotyls and has become bicarpellate. Now in various species of Acer, tricarpellate ovularies and fruits frequently appear and sometimes even four perfect carpels may be present. The evolutionary change from three carpels to two carpels is again such that the reaction is not always perfect and a reversion to the more primitive condition takes place, not because of a mutative loss of the factor but merely because of a failure to react properly in the given physiological condition of the cells involved. Thus the old reaction, which was never lost, comes into play again. Similar reversions are seen in many other plants. *Juglans regia* L. frequently has tricarpellate gynecia.

Another good example of the imperfect development of an important potentiality in its first phylogenetic stages is the genus Arisaema. The lowest Aroids have bisporangiate flowers while the remaining ones are monecious with the exception of Arisaema, which contains both monecious and diecious species. In some of the monecious species, as in *A. dracontium* (L.) Schott., the plant is easily reversed from moneciousness to a staminate condition or from staminate to monecious. With greater difficulty the monecious condition can be caused to

approach a nearly complete carpellate condition. *A. triphyllum* (L.) Torr. is more decidedly diecious and is perfectly balanced so that the sex-reversal can be easily induced in either direction from the one sexual state to the other or to moneciousness. It is said that some species of Arisaema are much more stable in their sexual states than is *A. triphyllum*.

The perfection principle and orthogenetic series are again illustrated by the splitting of the husk of the fruit in the genus Hicoria. In *Juglans regia* L. the husk separates from the nut or pit as in a hickory but does not split. In *Hicoria cordiformis* (Wang.) Britt. the husk is tardily four-valved. In *H. microcarpa* (Nutt.) Britt. the husk splits tardily and incompletely to the base. In *H. villosa* (Sarg.) Ashe. the husk splits partly to the base. In *H. ovata* (Mill.) Britt. the husk is thick and soon splits into four valves to the base. In *H. carolinaeseptemtrionalis* Ashe. the husk soon splits completely and falls readily into four valves or pieces.

The Nymphaeales as well as certain other groups show a progressive, perfective series in the evolution of staminodes. In Brassenia and Cabomba, which have the lowest apocarpous, hypogynous type of flower, there is no sign of any disturbance between the perianth and andrecium. In *Nymphaea advena* Sol., with a syncarpous, hypogynous flower, there is a slight development of staminodes at the base of the andrecium, usually confined to the outermost members. These stamens are slightly enlarged, flattened structures which still show vestigial microsporangia and have only a slight degree of petal characteristics. In *Castalia odorata* (Dry.) W. & W., which has a syncarpous flower in the first stage of epigyny, there is a prominent zone of staminodes, ranging from typical petals at the outer margin to typical stamens at the inner margin, between the true corolla and the normal stamens. Finally in *Victoria regia* Lindl., which belongs to the epigynous Nymphaeaceae with epigynous hypanthium, the development of petal-like staminodes is more extreme even than in Castalia.

In the Apocynaceae and Asclepiadaceae, the bicarpellate ovulary undergoes a characteristic splitting which sometimes includes even part of the style. These separated carpels develop into two follicles. The splitting is a secondary character evolved in the syncarpous condition. In some Apocynaceae the carpels are not thus split apart but continue in the same general condition as all the lower Tubiflorae.

Apocynum is a genus in which definite splitting occurs. Now in studying the development of the fruit of species of this genus it was found that *A. cannabinum* L. sometimes develops fruit to maturity without any splitting taking place. This again illustrates the principle that those groups or species which represent the first steps of an evolutionary series do not have the potentiality in as definite and perfect a state as those more advanced in the series. In Asclepias the splitting apparently occurs regularly, although no extensive observations have been undertaken to determine this definitely.

In both Monocotyls and Dicotyls, the co-ordinating reactions in the stem bud, which determine the position of the leaves, frequently indicate a definite evolutionary movement from a several-spiral condition to a two-ranked condition or unaspiral as the determinate culmination type. The Monocotyl lines nearly all end in a unaspiral. The three closely related genera of Fagaceae, Quercus, Castanea, and Fagus, show a perfective movement toward a definite, two-ranked reaction potentiality. *Quercus muhlenbergii* Engelm. and other species do not have a two ranked leaf arrangement but a typical 2–3 spiral system. The winter bud scales also indicate a primitive condition, having a 2–3 spiral system with 5 spiral radii in evidence. In *Castanea dentata* (Marsh.) Borkh. some of the twigs have two-ranked leaves and some have a more primitive spiral system like the oak. The two kinds of branches appear on the same tree. The potentiality for two-ranked has been acquired but often fails to come into play. In *Fagus grandifolia* Ehrh. the leaf arrangement is regularly and perfectly two-ranked under all ordinary conditions. In this series the movement is from no two-ranked potentiality, to a potentiality for the two-ranked expression which is decidedly unreliable and indefinite, to a two-ranked potentiality which is of such a nature that the hereditary expression is perfect in all ordinary physiological-ecological conditions. The characters of the fruit cups and involucres and of the staminate catkins also determine the progressive phylogenetic series as (1) Quercus, (2) Castanea, (3) Fagus independently of the orthogenetic series shown by the leaf arrangement.

THE PERFECTION PRINCIPLE ILLUSTRATED BY THE EVOLUTION OF AN ISOBILATERAL SYSTEM

The typical isobilateral flower is a rare type. It is ideally developed in the Fumariaceae. This type of symmetry is

gradually evolved as one passes from the lower Papaveraceae into the middle of the Fumariaceae. It is also developed in the Brassicaceae and Capparidaceae but not to such an extreme condition. An isobilateral flower or organ may be defined as one that can be cut into equal halves by two planes, intersecting at right angles, the halves of the one plane being unlike those of the other. In typical cases there is a reduction in the one plane as compared with the other. Often, both the number of parts and the forms and peculiarities of the non-corresponding halves are different.

In the lowest Papaveraceae, the entire flower shows nothing but the primitive spiral and cyclic, radial symmetry. There is no evidence of bilaterality of any kind. *Romneya coulteri* Harv., the matilija poppy of southern California, is described as having constantly 3 sepals, 3+3 petals, many stamens, and numerous united carpels. I have not had the opportunity to study this species. *Platystemon californicum* Benth. has a similar structure with 3 sepals, 3+3 petals, 42, more or less, stamens, and 6–18 carpels.

In *Argemone intermedia* Sweet, White Prickly-poppy (Figs. 1, 2), a common species of the western prairie and plains, the majority of flowers on a plant usually have the primitive trimerous perianth, 3 sepals, and 3+3 petals, with a very variable number of stamens, 184–336, and 2–6 carpels. Fig. 1 represents a typical actinomorphic flower, while Fig. 2 represents a rather reduced isobilateral type. These two types of flowers occur on the same plant but the radially symmetrical ones are much more abundant than the isobilateral ones. The species represents a plant that has taken the first step toward the isobilateral condition and the new character is very unreliable in expression. It is not a matter of hereditary segregation but one of hereditary expression, and the old trimerous heredity in the great majority of flower buds comes to activity rather than the new. The principle of imperfection is strikingly in evidence.

The commonly cultivated oriental poppy, *Papaver orientale* L. (Figs. 3, 4) is somewhat farther along the road toward isobilaterality. Sometimes the flowers with actinomorphic perianths and with isobilateral perianths are produced about equally, but at other times either the isobilateral or the actinomorphic type is the more abundant. As in *Argemone intermedia* both types of flowers are commonly produced on the same

plant. In the general advancement of determinateness the oriental poppy is still in the more primitive condition both in respect to stamens, 390–450 ±, and carpels, 10–15 ±.

The more typical poppies have an isobilateral perianth with 2 sepals and 2+2 petals quite regularly. *Papaver dubium* L. (Fig. 5) is of this type, with an isobilateral perianth, 232 ± stamens, and 7 ± carpels (6–10). In general the flower is decidedly reduced when compared with *P. orientale.*

In *Stylophorum diphyllum* (Mx.) Nutt. (Fig. 6) the flower again shows a decided reduction over that of *Papaver dubium,* having 2 sepals, 2+2 petals, 72 ± stamens and only 4 carpels, or sometimes these are reduced to 3 or 2. *Chelidonium majus* L. (Fig. 7) is approaching quite near to the perfect isobilateral type with 2 sepals, 2+2 petals, 2 carpels and only 16 ± stamens (14–24).

Passing over to the Fumariaceae, we find the isobilateral symmetry perfectly developed. In the Dutchman's-breeches, *Bicucula cucularia* (L.) Millsp., the flower (Fig. 8) has 2 sepals, 2+2 petals, 2+4 stamens and 2 carpels. The isobilateral movement has finally attained mathematical perfection. The two outer petals are spurred while the two inner ones have no spurs. A somewhat similar condition is developed in some Brassicaceae, but to a decidedly less extent, as in *Cheiranthus cheiri* L., *Ricotia lunaria* DC., and *Lunaria annua* L. While the flower has progressed to ideal isobilaterality, the fundamental progression of more prompt determination of the floral axis in relation to the beginning of the reproductive reactions has continued, and in the Bicucula type the upper 4 stamens are reduced as compared with the 2 lower ones, having only 2 microsporangia while the lower ones have the usual 4 microsporangia. This is a characteristic example of the way characters evolve as the result of some fundamental orthogenetic movement and not through natural selection in a life and death struggle nor as a response to use and disuse. It would certainly require a marvelously credulous mind to see any advantage in having the 2 outer stamens developed with 4 sporangia and the 4 inner stamens with only 2 sporangia each. This peculiarity is present in other genera of the family. Great numbers of similar situations are in evidence when one makes a proper taxonomic analysis of the various plant groups. Now the general orthogenetic movement of the time of floral determination could be carried still further and there are genera with

more reduced numbers. In the Brassicaceae the isobilateral flower is sometimes reduced to the formula—sepals 4, petals 0, stamens 2, carpels 2, as in *Lepidium ruderale* L.

In the Fumariaceae, a new evolutionary trend is introduced in some species, namely, a zygomorphic potentiality which is imposed upon the isobilateral condition. A typical example is presented by *Capnoides aureum* (Willd.) Ktz. (Fig. 9). Structurally the flower is isobilateral in even a greater degree than in Bicucula, having the 6 stamens united by their filaments into 2 groups. The outer pair of petals show a strong zygomorphy in that one is spurred and the other is not. There is also a nectar gland at the base of the spurred petal and none at the base of the opposite petal. This flower series, therefore, shows the general evolutionary series of the poppy-fumatory group to have progressed from a slow, variable determination to a prompt, definite determination; from spiral to cyclic; from actinomorphic to isobilateral; and finally from the isobilateral to the zygomorphic condition. Usually the advanced movement is from actinomorphy directly to zygomorphy; and then rarely an unsymmetrical condition of form and general expression may be added on top of the zygomorphic condition.

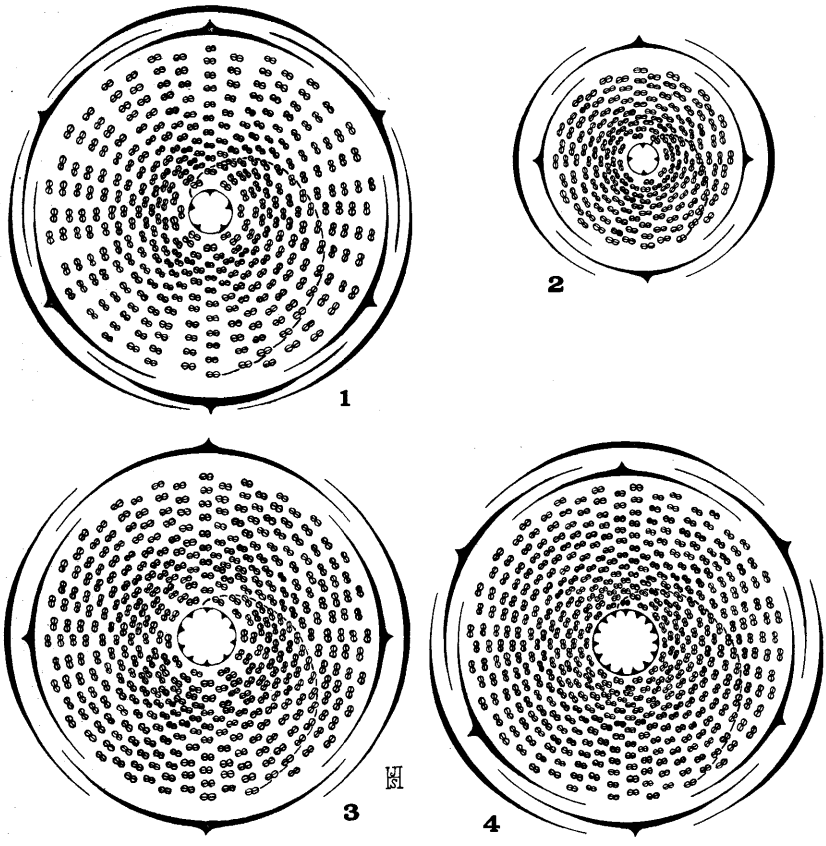
To some, the term perfective, or perfection, more commonly conveys the idea of an immediate ideal goal or attainment; and from a utilitarian standpoint of evolution such might be the inference. But aside from a philosophical attitude one may have in asserting that there is in the organic world a system and principle which does bring about an orderly cosmos and a highly successful balance of nature, this idea should not be entertained in relation to the scientific study of the perfective development of characters and properties of organisms. As intimated in at least one example of perfective evolution given above, the result may be a decided disadvantage to the individual in relation to its environment, or the mechanism may be highly perfected and still be of no use whatever to its possessor. In this world, a thief may attain perfection in his calling as well as a saint. However, in its broadest aspects, the general course of evolution is perfective in the ethical and altruistic sense, at least to all people so philosophically inclined as to be able to view the system as a whole.

SUMMARY STATEMENT

There is a manifest tendency toward progression and perfective development in the evolution of many fundamental plant series. This progression in perfection of structures and reactions is not to be ascribed to any selective principle nor to any direct reaction to a series of changing environments, either in time or space, but to some internal cause dependent on the nature of the protoplasm involved.

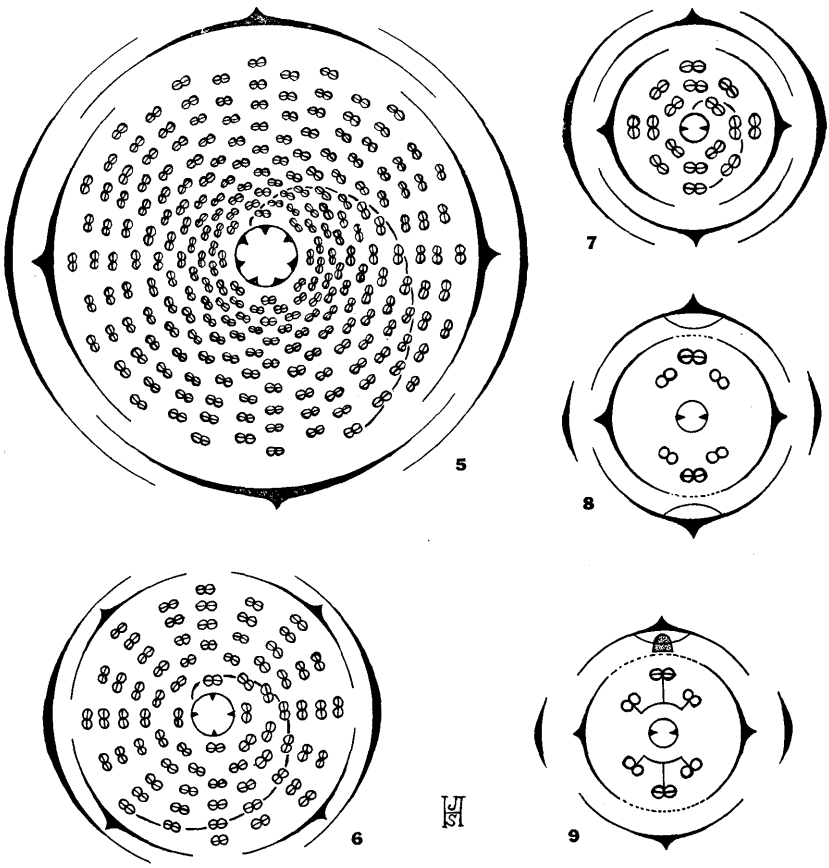
Among the more important examples discussed, in the present paper, of evolutionary series showing progressive, more dependable, and more prompt reaction in passing from the lower to the higher members are the following: Progression in the definiteness of differentiation expression in sporophyll and foliage leaf. Evolution of definiteness and promptness of determination of the floral axis. The more definite determination of the inflorescence axis in the higher as compared with the more primitive types of inflorescence heads. The instability of the reaction on the lower evolutionary levels in passing from a five-parted to a four-parted flower in various dicotyls. The decided perfective tendency in the progressive evolution of zygomorphy. The progressive and perfective series shown in the evolution of the isobilateral type of flower from the more primitive actinomorphic type in the Papaveraceae-Fumariaceae group.

The facts presented, together with a large array of similar phenomena which might be adduced, indicate decidedly the presence of an internal perfective principle operative in the evolution of organisms and that evolution in its fundamental aspects is intrinsic, orthogenetic, progressive, perfective and determinative.



Diagrams of floral structures in the isobilateral series in Papaveraceae and Fumariaceae.

1. *Argemone intermedia* Sweet. Sepals 3, petals 3+3, stamens 336, carpels 5. Actinomorphic.
2. *Argemone intermedia* Sweet. Sepals 2, petals 2+2, stamens 184, carpels 4. Isobilateral.
3. *Papaver orientale* L. Sepals 2, petals 2+2, stamens 390, carpels 10. Isobilateral.
4. *Papaver orientale* L. Sepals 3, petals 3+3, stamens 450, carpels 15. Actinomorphic.



Diagrams of floral structures in the isobilateral series in Papaveraceae and Fumariaceae.

5. *Papaver dubium* L. Sepals 2, petals 2+2, stamens 232, carpels 7. Isobilateral.
6. *Stylophorum diphyllum* (Mx.) Nutt. Sepals 2, petals 4, stamens 72, carpels 4. Isobilateral.
7. *Chelidonium majus* L. Sepals 2, petals 2+2, stamens 16, carpels 2. Isobilateral.
8. *Bicucula cucularia* (L.) Millsp. Sepals 2, petals 2+2, stamens 2+4, carpels 2. Perfectly isobilateral.
9. *Capnoides aureum* (Willd.) Ktz. Sepals 2, petals 2+2, stamens 2+4, carpels 2. Isobilateral-zygomorphic type.